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The Origin of Asplenium ebenoides

BY MARGARET SLOSSON

The question whether *Asplenium ebenoides* R. R. Scott is or is not a hybrid between *Asplenium platyneuron* (L.) Oakes and *Camptosorus rhizophyllus* (L.) Link has long been a vexed one. In order to ascertain the truth by crossing *A. platyneuron* and *C. rhizophyllus*, I began experiments several years ago which had been suggested by Mr. George E. Davenport.* Partial description of these experiments, together with a discussion of the advantages and disadvantages of various methods of attempting the hybridizing of ferns, has been announced already, † but it is necessary to refer here to the method that Mr. Davenport suggested and which, with slight modification, was at first adopted.

This method consists of dividing prothalli of two species between the archegonial and antheridial regions before fertilization has taken place and planting the archegonial section of a prothallus of one of the species close to the antheridial section of a prothallus of the other, so that antheridia and archegonia come in contact. The idea is that should fertilization subsequently take place it can only be cross-fertilization and the resultant plant a hybrid. It should be said that although the formation of plants of pure species from asexual growth, which sometimes occurs on prothalli, would not be prevented, yet plants arising in this way can be distinguished, according to Dr. Farlow, from plants springing from fertilized archegonia and can, therefore, be detected and removed.

On experimenting, however, two objections to this method were encountered: (1) Nearly all of the sections of prothalli

* Papers Pres. Boston Meet. (1898), 9. 1899.

† Fernwort Papers (ined.).

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sent out branches and it appeared extremely probable that on the branches the organs that had been removed were often regenerated. Each of the branches was shaped more or less like a complete prothallus, and many produced plants of pure species borne, as in the normal prothalli, close to a sinus. I did not wish to disturb the cultures sufficiently to make certain, but it is not probable that all, if any, of these plants were the result of asexual growth; (2) Very many of the antheridial sections, though possessing roots when planted, either died immediately or appeared to fade and remain faded for weeks, reviving only by sending out branches. The archegonial sections, on the contrary, though rootless when planted, as a rule quickly produced roots and grew rapidly.

Since there appears to be no way of dividing prothalli that offers any certainty that the organs cut away will not be regenerated, it is evident that in attempting to cross species of ferns that method of dividing and bringing prothalli together is best in which the prothalli offer most quickly facilities for cross-fertilization, in order that it may take place before regeneration of the organs. As antheridial sections that die or fade cannot be said to offer such facilities, in the experiments described further on whole prothalli have been substituted for the antheridial sections. In cutting the archegonial sections the incision has been made transversely close to the sinus of each prothallus in order to make certain of retaining archegonia only on the archegonial sections. Then, discarding the section containing antheridia, the archegonial section of a prothallus of one species has been planted against a whole pro-

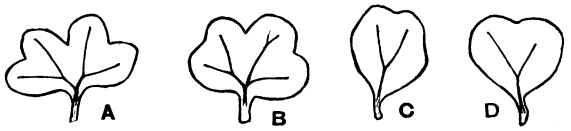


FIG. 1. × 4. The letters in the series uniformly refer to the same plants: *A*, *Asplenium platyneuron*; *B*, hybrid artificially produced; *C*, *Asplenium ebenoides*; *D*, *Camptosorus rhizophyllus*.

thallus of the other species with the lower surfaces of the prothalli pressed close together, in the hope that when antherozoids should be set free on the whole prothallus some would reach and cross-

fertilize the archegonia on the archegonial section before that section could regenerate antheridia of its own.

It is obvious that in seeking to discover the origin of *A. ebenoides* the removal of organs of *A. platyneuron* or *C. rhizophyllus* is only of use in so far as it may facilitate cross-fertilization, for *A. ebenoides*, while it combines characteristics of these two ferns and hence might be produced by their cross-fertilization, is so distinct from either that it could not possibly be produced by the cross-fertilization of either. For the same reason it could not be produced by the asexual growth of either. Therefore if a plant of *A. ebenoides* should spring from prothalli of *A. platyneuron* and *C. rhizophyllus* that had been planted together and pure cultures had been insured, that plant must be considered proof that *A. ebenoides* is a hybrid between *A. platyneuron* and *C. rhizophyllus*.

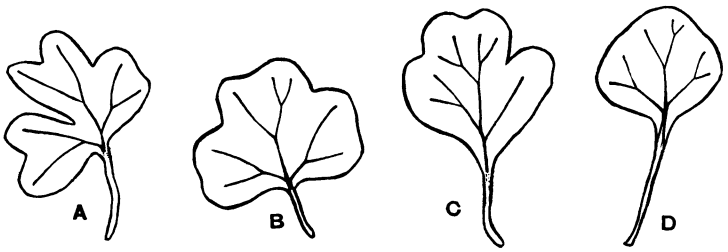


FIG. 2. × 4.

In order to insure pure cultures, in my experiments the prothalli have been raised on sterilized earth in new flower-pots and kept under glass. Lack of success during several years in crossing *A. platyneuron* and *C. rhizophyllus* has not been caused by prothalli of these ferns failing to produce a hybrid when planted together, but by the difficulty in getting prothalli of both ferns in proper condition at the same time in order to plant them together. Almost as soon as that was overcome results followed.

In the winter of 1900–1901 spores of these two ferns sown in separate flower-pots developed prothalli in large numbers. During February and March archegonial sections were cut from the prothalli of *C. rhizophyllus*, planted in a third pot, and a whole prothallus of *A. platyneuron* planted close against each section. In a fourth pot archegonial sections of *A. platyneuron* were planted

against whole prothalli of *C. rhizophyllus*. In a fifth pot a few whole prothalli of both ferns were planted against each other. In all about fifty pairs of prothalli were planted.

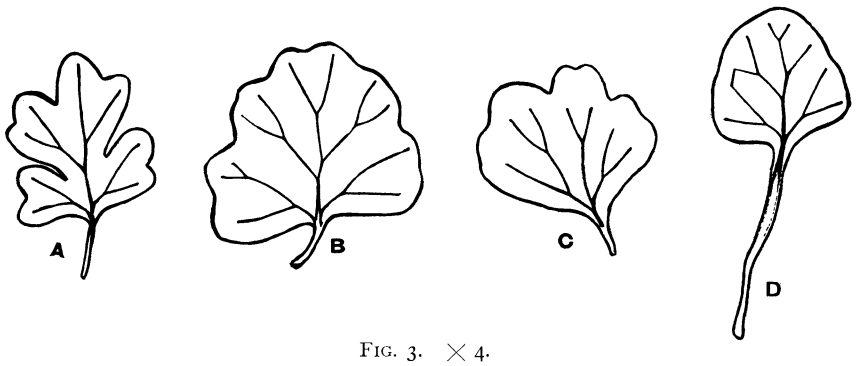


FIG. 3. × 4.

Now, if in the third pot antherozoids were set free on one of the whole prothalli of *A. platyneuron* and some were to fertilize the archegonia on the archegonial section of *C. rhizophyllus* in contact with that prothallus, in all probability some also would fertilize the archegonia on the whole prothallus. Hence, should a hybrid-plant develop, we would expect a plant of pure *A. platyneuron* to

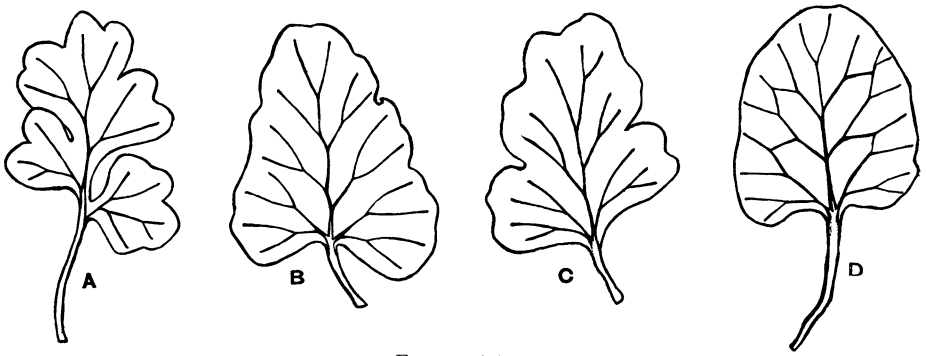


FIG. 4. × 4.

develop at the same time. That is what occurred. In June a plant, unquestionably a hybrid between *A. platyneuron* and *C. rhizophyllus*, and a plant of pure *A. platyneuron* sprang up side by

side.* It is probable, then, that this hybrid-plant was produced by archegonia of *C. rhizophyllus* fertilized by antherozoids of *A. platyneuron.* The following September a second hybrid-plant sprang up, but, as in the meanwhile plants both of pure *A. platyneuron* and of pure *C. rhizophyllus* had been produced, the organs cut away had probably been regenerated, hence no conclusions can be formed as to whether this second plant is the result of the same cross as the first or of the reciprocal cross.

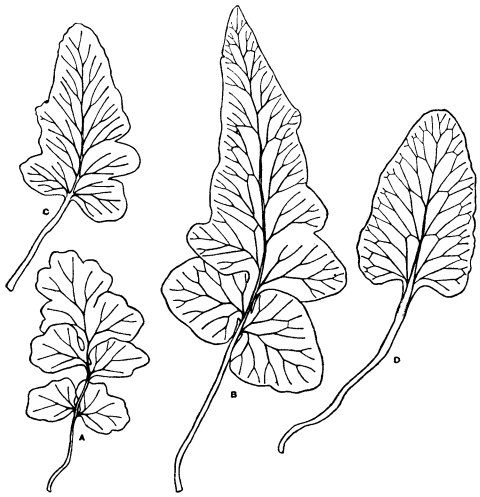


FIG. 5. × 1½.

Shortly before September, from the appearance of plants of pure *C. rhizophyllus* and pure *A. platyneuron* in the fourth pot, it became evident that in that also the organs cut away had probably been regenerated, so for convenience the contents of the fifth pot were transferred to the fourth one. Two hybrid plants sprang up in it soon afterward, about the same time that the second hybrid plant appeared in the pot with the June plant.

The only fact that could lead one to suppose that the hybrid plants in the two pots might represent reciprocal crosses is that in the one containing the June plant the leaves of both plants, when young, were truncate at the base, like leaves of young *A. platy-*

* In this connection it is interesting to note that a pocket of rock containing a plant of *A. ebenoides*, found by G. A. Woolson in Vermont, contained also a plant of *A. platyneuron.*

neuron, and in the other cuneate, like leaves of young *C. rhizophyllus*. Later, the leaves of all four became cordate at the base, like leaves of mature *C. rhizophyllus*.

There can be no doubt of the hybridity of these four plants: they have shown from the beginning a most curious combination of the characteristics of *A. platyneuron* and *C. rhizophyllus*.

The leaves have varied from suberect to almost decumbent and, though none have taken root, some have rested their tips upon the earth.

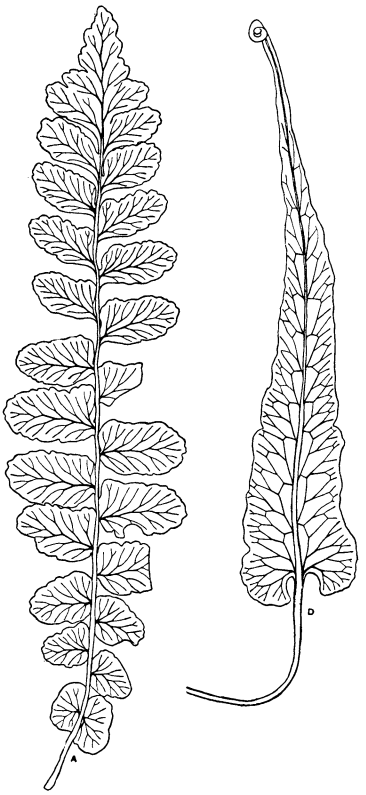


FIG. 6. × 1½.

That the leaf-blades are intermediate in outline between the leaf-blades of *A. platyneuron* and *C. rhizophyllus* may be seen from figures 1–7, in which the three ferns are shown in somewhat parallel stages of development, *A* representing leaves of *A. platyneuron*, *B* and *BB* in *f.* 1, 2, 3, 4 and 7 leaves of the June plant of the hybrid, *B* in *f.* 5 a leaf, of one of the September plants of the hybrid from the fourth flower-pot, and *D* leaves of *C. rhizophyllus*. The blades of the leaves of the hybrid combine fairly their texture, which is characteristic of *A. platyneuron* but not of *C. rhizophyllus*, with veins forming slightly raised lines on the face of the leaf, which is characteristic of *C. rhizophyllus* but not of *A. platyneuron*. Their color, though a lighter and brighter green than that of *C. rhizophyllus*, suggests it.

In one of the hybrid-plants in each pot the veins have been wholly free, and in the other, especially in the June plant, the veins, though mostly free, have formed a number of areolae.

In all three ferns when very young the petioles are green,

but other coloring soon appears at their bases and spreads upward. In *A. platyneuron* this coloring is at first light stramineous and spreads rapidly, involves in time the entire rachis and turns chestnut brown or purplish-ebeneous, sometimes leaving touches of green. In *C. rhizophyllus* it seems to vary from light to dark brown and extends, ultimately, only part way up the petiole. In the hybrid it has been brown from the beginning, has now a dark purplish tinge, and extends some distance up the back of the rachis. The petioles themselves in *C. rhizophyllus* are more or less narrowly winged on the sides, in the hybrid, they are similar, though perhaps more slender, while in *A. platyneuron* they are wingless.

The scales clothing the bases of the petioles in the three ferns are minute, acuminate, and reticulate in reddish-brown on an almost colorless background. In *C. rhizophyllus* they vary from lanceolate to lanceolate-deltoid or are occasionally ovate at base and narrowed suddenly above, and their margins are entire or sometimes bear short cilia. In *A. platyneuron* they are elongate-linear or lance-linear and their margins bear cilia often long and conspicuous. In the hybrid they are more or less intermediate in shape, resembling occasionally the scales of one parent more than those of the other, and their margins are entire or bear cilia varying in length.

On comparing the hybrid plants with a large number of specimens of *Asplenium ebenoides* from Havana Glen, Alabama, and from Virginia, and with photographs of *A. ebenoides* from Virginia, Maryland, and Vermont, I find that the characteristics of the hybrid are, with one exception, characteristics also of *A. ebenoides*. This exception is the manner in which the base of the blade of the leaf varies, at different stages of development, in its resemblance to that of *A. platyneuron* or of *C. rhizophyllus*. As already stated, in two of the plants of the hybrid when young the base of the blade resembled that of young *A. platyneuron* and in the other two that of young *C. rhizophyllus*, while in all four when older it resembled that of mature *C. rhizophyllus*. In young specimens of *A. ebenoides* from Havana Glen, the only young wild plant of this fern I have seen, the base of the blade resembles that of young *C. rhizophyllus*, while in older plants from Havana Glen

and elsewhere it resembles in some of the leaves that of mature *C. rhizophyllus* and in others that of mature *A. platyneuron.* But, supposing *A. ebenoides* and the hybrid to have arisen in the same way, for some of the progeny of the same parents to resemble one parent and for others at the same stage of development to resemble the other, is so common an occurrence that no comment is required. From the figures, in which *C* and *CC* represent leaves of *A. ebenoides* from Havana Glen, this varying resemblance of *A. ebenoides* and of the hybrid, at various stages of development, to *C. rhizophyllus* or *A. platyneuron* may be seen. It is especially noticeable in figures 1–3.

Of characteristics possessed by *A. ebenoides* and not by the hybrid I find but two:

1. Possession of sori. The lack of this characteristic in the hybrid is easily accounted for by the age of the plants. The plant are still growing and it is confidently expected that sori will develop upon older leaves.

2. Elongation and attenuation of the pinnae. But this characteristic is either not constant in *A. ebenoides* or else appears in different plants at different stages of development. It is very marked and seems to appear, as a rule, at an early age, in most specimens of *A. ebenoides* from Havana Glen. On the other hand, Dr. Murrill tells me that it did not appear in his plants from Virginia until they had been kept for some time in a greenhouse, in a favorable environment which caused them to develop luxuriantly. In one of his specimens that show no trace of it the blade of the leaf is fully 10.797 cm. long, about a third longer than that of the largest leaf of the hybrid plants, and well fruited. None of the leaves of the specimens of *A. ebenoides* found by Dr. C. E. Waters in Maryland show elongation and attenuation of the pinnae. So the utmost that can be said of the lack of this characteristic in the leaves of the hybrid is that they resemble some leaves of *A. ebenoides* rather than others. How close the resemblance is may be seen by comparing *B* and *BB, f.* 7, which represent leaves of the hybrid, with *C* and *CC, f.* 7, which represent leaves of *A. ebenoides.*

Thus, on comparing with *A. ebenoides* a fern produced by crossing *A. platyneuron* and *C. rhizophyllus,* it is found similar to

A. ebenoides in habit, coloring, texture, form of the leaf, venation, and character of the scales ; in short, it does not possess one characteristic that *A. ebenoides* does not possess at some time in its life history, and, though young, lacks of the characteristics of *A. ebenoides* only the possession of sori and elongation and attenuation of the pinnae, both of which are often absent in *A. ebenoides* at the same age. Surely we have here convincing proof of the origin of *A. ebenoides.*

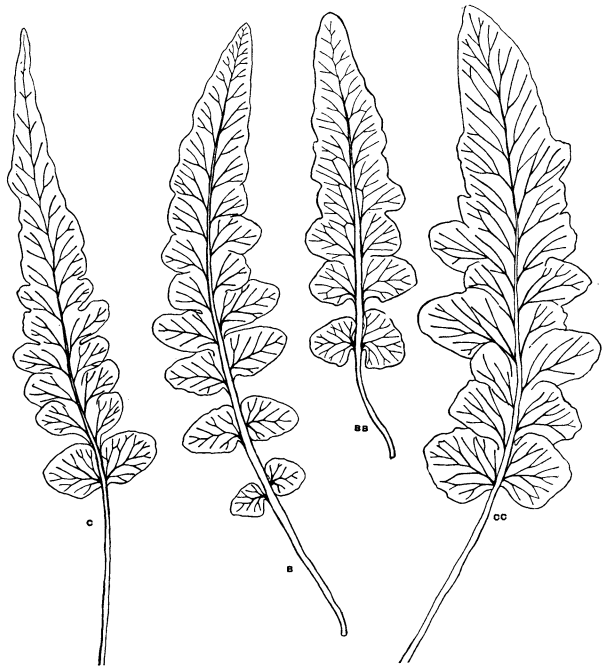


FIG. 7. × 1½.

I am indebted to Dr. Lucien M. Underwood not only for the privilege of examining his collection of specimens of *A. ebenoides* from Havana Glen, but also for many courtesies extended to me in the preparation of this paper ; to Mr. William R. Maxon for a generous number of additional specimens of *A. ebenoides* from Havana Glen ; to Dr. W. A. Murrill for a photograph of *A. ebenoides* from Virginia and the loan of specimens and manuscript notes ; to Dr. H. H. Swift for photographs of *A. ebenoides* from Vermont, and to Dr. C. E. Waters for photographs of *A. ebenoides* from Maryland.